PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

Vol. 42, No. 21, pp. 525-535, 33 figs.

May 14, 1982

LATE MIOCENE BALANID CIRRIPEDIA FROM THE BASAL WILSON RANCH BEDS ("MERCED" FORMATION), SONOMA COUNTY, NORTHERN CALIFORNIA

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ABSTRACT: The basal conglomerate of the Wilson Ranch beds (Merced Formation of authors) contains abundant barnacle remains including three identifiable species of the family Balanidae. Balanus sp. aff. B. nubilus Darwin, 1854, is similar to extant B. nubilus and the California late Miocene-early Pliocene species B. proxinubilus Zullo, 1979, but differs in the internal morphology of the scutum. Balanus irradians new species is a member of the Balanus balanus (Linnaeus, 1758) complex distinguished by its lack of radii. Notomegabalanus(?) insperatus new species is a megabalanine with Southern Hemisphere cool-temperate affinities distinguished by its prominently ribbed parietes. A late Miocene age is assigned to the basal conglomerate on the basis of its stratigraphic relationship to a radiometrically dated tuff within the Wilson Ranch beds and on biostratigraphic evaluation of the molluscan fauna. The fauna of the basal conglomerate suggests deposition in an immediately subtidal environment subjected to wave and current action, and a cool temperate marine hydroclimate.

INTRODUCTION

A fossiliferous marine conglomerate of late Miocene age in southwestern Sonoma County, northern California (Fig. 1) contains an abundance of balanid barnacle remains. The specimens consist of shells, disarticulated compartmental plates, and a few dissociated scuta representing four species. One of these species cannot be identified beyond the generic level. A second is similar to, but not conspecific with, the extant Pacific coast species *Balanus nubilus* Darwin, 1854. The third, based on shell characters alone, is sufficiently unique to permit its description as a new species with affinities to the modern *Balanus balanus* (Linnaeus, 1758) complex. The fourth is a new species of megabalanine that appears to represent one of the newly delimited extant austral genera.

STRATIGRAPHY

Outcrops of marine sandstone in southwestern Sonoma County were for many years considered correlatives of the type Merced Formation of the San Francisco peninsula and



FIGURE 1. General locality map for CASG locality 54135, lower Wilson Ranch beds, southwestern Sonoma County, California.

referred to that unit (e.g., Dickerson 1922; Weaver 1949; Travis 1952). Higgins (1960) documented lithologic and faunistic differences between the type Merced Formation and the Sonoma deposits, and provided compelling arguments that the two units were deposited in separate basins. Higgins, however, did not propose a separate formational name for the Sonoma County deposits.

A tuff interbedded with the sandstone was described by Osmont (1905) as the Sonoma Tuff. In ensuing years, following the work of Dickerson (1922), the name Sonoma has been used to refer to the Neogene volcanic assemblage of eastern Sonoma and Napa counties. The original Sonoma Tuff can be regarded as one of a series of tuffaceous intertongues of the eastern volcanic assemblage into the western marine sequence. Osmont (1905) also described a molluscan fossil locality in the marine sandstone containing the Sonoma Tuff, to which he applied the name Wilson Ranch beds. As this is the earliest formal stratigraphic name that has been used for this Neogene marine unit, we will refer to these deposits as the Wilson Ranch beds.

K-Ar dates from the pumiceous, vitric tuff interbed described by Osmont have given an age range of 5.7 ± 0.6 to 6.1 ± 0.1 m.y. (Sarna-Wojcicki 1976). Bartow and others (1973) reported molluscan assemblages in the Wilson Ranch beds that ranged in age from the early Pliocene below, to late Pliocene above the dated tuff. The early and late Pliocene molluscan assemblages were correlated with Hemphillian (late Miocene to early Pliocene) and Blancan (late Pliocene to early Pleistocene) land mammal assemblages, respectively, from the Petaluma Formation immediately to the east. These relative ages are in terms of conventional Pacific coast usage. If, however, 5.0 m.y. is acceptable as the age of the Miocene-Pliocene boundary as proposed by Berggren (1972, 1978) and Van Evsinga (1975), then that part of the Wilson Ranch beds below the dated tuff is of Miocene age. This conclusion is supported by biostratigraphic evaluation of the molluscan fauna by Barry Roth (California Academy of Sciences, pers, commun., 1981). Roth would correlate the lower Wilson Ranch beds with the Pancho Rico Formation of Monterey County, California, which he and others now regard as late Miocene in age (Addicott 1976; Roth and Guruswami-Naidu 1978).

The barnacles described herein are from California Academy of Sciences Department of Geology (CASG) locality 54135. This locality is in a coquina near the top of the basal conglomerate of the Wilson Ranch beds in the Two Rock quadrangle, U.S. Geological Survey 7.5' series, 1954 edition, revised 1971, and is in that part of the section referred by Osmont (1905) to the San Pablo Formation of the eastern San Francisco Bay region. A precise locality description is on file with the Department of Geology. At the exposure containing CASG locality 54135, the Wilson Ranch beds unconformably overlie the Franciscan assemblage (Fig. 2). The basal 0.5 m consists of a fining-upwards conglomerate composed of coarse sand, rounded pebbles, and angular pebble- to cobble-sized fragments of Franciscan-assemblage rocks in a fine-grained sandstone matrix. The upper part of the conglomerate is the coquina (CASG locality 54135) which is composed of predominantly horizontally bedded invertebrate shells. A vertebrate

fossil lag, consisting of scattered intact elements and abundant, well-rounded bone fragments, overlies the coquina. The vertebrate lag grades upward into 3.4 m of massive, moderately indurated, fine-grained sandstone containing scattered invertebrates and rare vertebrate remains. This sandstone is overlain by tuffaceous sandstone to the top of the exposure. The basal conglomerate at this locality is estimated to be 50 m stratigraphically below the dated tuff in the Wilson Ranch beds (Peter Rodda, California Academy of Sciences, pers. commun., 1981).

PALEOECOLOGY

The petrology and fauna of the basal conglomerate suggest that the barnacles inhabited a rocky intertidal or immediately subtidal environment exposed to moderate or heavy surf. The coquina itself, and its relationship to the underlying fining-upwards conglomerate, suggest a time of stillstand after rapid transgression in a shallow depositional basin affected by wave base and/or current action. According to Barry Roth (pers. commun., 1981) the molluscan fauna suggests a marine hydroclimate similar to that of modern Puget Sound (i.e., cool temperate). These environmental conditions are supported by the composition, morphology, and preservation of the barnacle fauna.

Systematic Account

Subclass CIRRIPEDIA Burmeister, 1834 Order THORACICA Darwin, 1854 Superfamily BALANOIDEA (Darwin), Newman and Ross, 1976 Family BALANIDAE Darwin, 1854 Subfamily BALANINAE Darwin, 1854

Balanus sp. aff. B. nubilus Darwin, 1854 (Figures 3-11)

Four complete shells, one partial shell, several disarticulated compartmental plates, one entire scutum, four fragmentary scuta, and a few fragments of basis from CASG locality 54135 are here referred to a species that is similar to, but probably not conspecific with, *Balanus nubilus*. The shells are conic, the radii are moderately well developed with oblique, jagged summits, and the orifice is toothed. The ribbing of the shell interior is not prominent, and the basis in larger individuals is cup-shaped and profusely porous near the margins. The parietal septa are

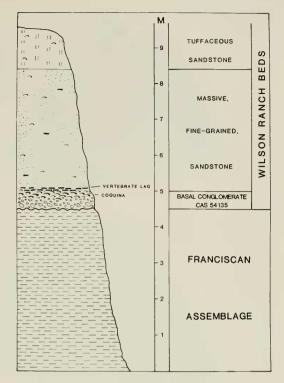
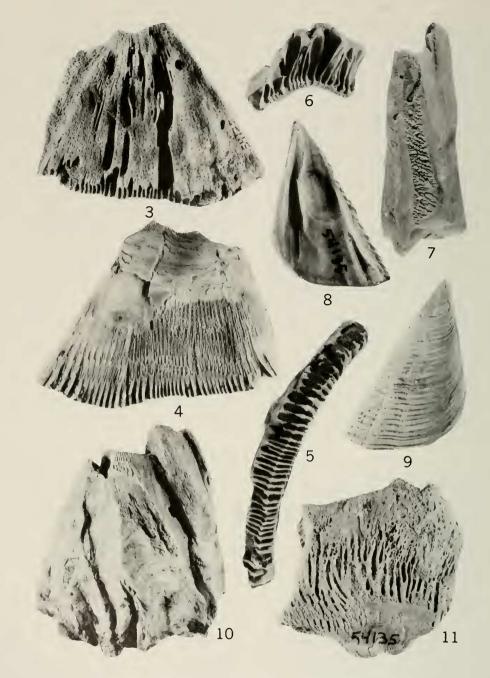


FIGURE 2. Stratigraphic setting for CASG locality 54135, lower Wilson Ranch beds, southwestern Sonoma County, California.

crowded and thin, and the narrow, elongate parietal tubes rarely possess transverse septa.

The scuta that appear to be associated with these shells are higher than wide, slightly bowed outwards near the apex, and with a slightly reflexed tergal margin. The exterior is ornamented by prominent, closely spaced growth ridges that are faintly crenate, and the basitergal angle is rounded. The articular ridge is short, less than one-half the length of the tergal margin, and slightly reflexed over the narrow, shallow, articular furrow. The adductor ridge is erect, highest along the margin of the large, oval, and deeply impressed adductor muscle pit, but extending both apically and basally beyond the boundaries of the adductor pit. The depressor muscle pit is large, triangular, shallow, and bordered on its occludent margin by a low ridge. The depressor muscle pit has one or more narrow, low longitudinal ridges within. The depressor muscle pit located at the basioccludent angle is triangularly



FIGURES 3-11. Balanus sp. aff. B. nubilus Darwin, 1854. Figs. 3-5. Exterior, interior, and basal views of lateral plate, hypotype CASG 60881; greatest height 47.5 mm. Figs. 6-7. Basal and alar sutural edge views of carinorostral and carinal plates, hypotype CASG 60882; greatest height 61 mm, greatest wall thickness 17 mm (note transverse septa in parietal tubes). Figs. 8-9. Interior and exterior views of scutum, hypotype CASG 60883; height 23 mm. Fig. 10. Side view of shell, hypotype CASG 60884; greatest height 49 mm. Fig. 11. Fragment of basis, hypotype CASG 60885; greatest diameter of fragment 35.5 mm.

elongate, deeply impressed, and partially overhung by the occludent margin of the plate.

The shell of this species is similar to that of Balanus nubilus and the related fossil species B. proxinubilus Zullo, 1979, from the upper Miocene Pancho Rico Formation of central California and the upper Pliocene San Diego Formation of southern California. The only qualitative difference is that the radii of the Wilson Ranch species appear to be consistently broader than those of either B. nubilus or B. proxinubilus. The Wilson Ranch scuta differ in having the adductor ridge separate from the articular ridge, and in the much shorter articular ridge. In this regard the internal morphology is somewhat similar to that of the scutum of B. rostratus Hoek, 1883, but the presence of vertical ridges or crests in the depressor muscle pit serves to distinguish the Wilson Ranch scuta and to suggest relationship with B. nubilus.

Balanus irradians new species (Figures 12-15, 18-21)

DIAGNOSIS.—Shell of six compartmental plates without radii; alae restricted to sheath area; sutures between compartmental plates obscured or represented by linear grooves; parietes with large, square to rectangular, transversely septate parietal tubes; number of interior ribs greater than number of parietal septa; basis calcareous, solid; distinguished from other members of the *Balanus balanus* complex by the lack of radii.

DESCRIPTION.—Shell thick, low to high conic or dome-shaped, with narrow carinolaterals and a small, untoothed, diamond-shaped orifice; sutures between the six compartmental plates obscured or represented by narrow grooves; radii absent; sutural edges between adjacent compartmental plates broad, bearing coarse, complexly arborescent denticulations; alae narrow, with horizontal summits, and restricted to region of sheath; exterior of parietes usually corroded; uncorroded parietes with external ornamentation of irregular, transverse growth rugae crossed by fine longitudinal striae; some specimens bear one to three external ribs on larger compartmental plates; length of sheath at least one-half height of compartmental plate; lower edge of sheath free-standing, acute, with cavity between it and interior of shell wall; interior of shell wall below sheath strongly ribbed, with the

largest internal ribs corresponding to the parietal septa, and from one to three smaller ribs between parietal septa; parietal tubes large, nearly square to rectangular, crossed by transverse septa and sometimes secondarily filled in upper third; parietal septa denticulate basally; inner surface of external lamina bears denticulae between parietal septa; basis calcareous, solid.

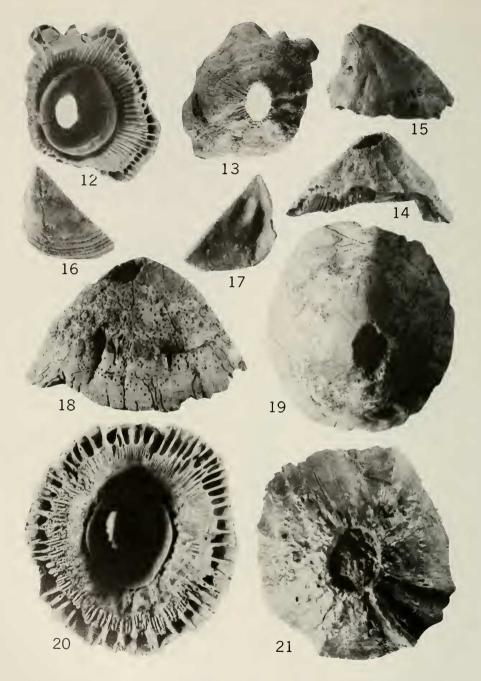
MATERIAL EXAMINED.—Twelve whole shells and 26 disarticulated compartmental plates from CASG locality 54135.

TYPE MATERIAL.—Holotype, CASG no. 60891; paratypes, CASG nos. 60892 through 60909, and paratype lot CASG no. 60910 in the California Academy of Sciences paleontological type collection.

ETYMOLOGY.—The specific name is derived from the Latin prefix *ir*-, without, and *radius*.

DISCUSSION .- Balanus irradians and the extant boreo-arctic species B. balanus and B. rostratus, constitute a small group in the genus Balanus that is characterized by solid, calcareous bases, large, square, parietal tubes, and secondary ribs between the primary septal ribs of the interior lamella of the parietal wall. The lack of radii and the overall morphology associated with a shell lacking radii are the major features distinguishing B. irradians from B. balanus and B. rostratus. In other respects, B. irradians shares characteristics with the extant species. The prominent external ribs present on some specimens are reminiscent of the ribbed wall of B. balanus, rather than the smooth shell of B. rostratus. On the other hand, both B, irradians and B. rostratus have transverse parietal septa that are lacking in B. balanus.

The corroded nature of the shells and the type of sediment in which they occur suggest that B. irradians lived in moderate- to high-energy environments. The thick shell wall, the suppression of radii, and the consequent development of a broad, coarsely denticulate sutural area for rigid articulation of the compartmental plates are comparable to shell development in species of Tetraclita Schumacher, 1817, that often inhabit areas of moderate to heavy wave shock and abrasion in the intertidal zone. A consequence of the lack of radii is that the orifice cannot be enlarged by lateral growth along the sutural edges of the plates as the shell increases in basal diameter and height. As Ross (1969) showed for Tetraclita, monometric growth forms enlarge their orifices by abrasion of the older, upper parts of the shell wall. The secondary filling and



FIGURES 12-21. Balanus irradians new species. Figs. 12-14. Basal, top, and side views of paratype CASG 60892; greatest diameter of base 29 mm, greatest height of shell 15 mm (note fragment of basis in upper part of Fig. 12). Fig. 15. Side view of shell, paratype CASG 60893; greatest height 13 mm. Figs. 16-17. Exterior and interior views of scutum tentatively identified with *B. irradians*, hypotype CASG 60920; height 10 mm. Figs. 18-20. Side, top, and basal view of shell, holotype CASG 60891; greatest height 24 mm, carinorostral diameter 38 mm. Fig. 21. Top view of eroded shell with prominent ribs, paratype CASG 60894; greatest diameter 38.3 mm.

the transverse septa of the parietal tubes prevent exposure of the internal tissues of the barnacle when the upper and outer shell wall are removed.

The affinities of *B. irradians* with *B. balanus* and B. rostratus are in keeping with the conclusion that the fauna of the basal Wilson Ranch beds lived in hydroclimatic conditions similar to those of modern Puget Sound. Balanus rostratus is a subtidal North Pacific boreo-arctic species ranging south to northern Japan in the west and to Puget Sound in the east. Balanus balanus is a lower intertidal and subtidal species of the Arctic, boreal Atlantic, and boreal Pacific, with a distribution similar to that of *B*, rostratus in the North Pacific. The fossil record of B. rostratus is limited to the late Pleistocene on the Pacific coast of North America where it is recorded as far south as central California (Zullo 1969b), but extends back to the Pliocene in Japan (Yamaguchi 1977). Balanus balanus is found in Pleistocene deposits of both the North Atlantic and North Pacific basins, but has not been recorded from deposits south of southern Oregon (Zullo 1969b). Miocene and Pliocene European records of *B*. *balanus* are spurious (Menesini 1968, in part), but the species does occur in glacio-marine sediments of the Miocene part of the Yakataga Formation in southeastern Alaska, and is reported from the Miocene of Japan by Yamaguchi (1971).

The morphology of *B. irradians*, particularly those features peculiar to this species, suggests that *B. irradians* is a derivative of either *B. balanus* or *B. rostratus*. The modifications seen in the new species reflect adaptations to life under conditions of pronounced wave shock and abrasion, perhaps in the intertidal zone in relatively open coastal conditions.

Balanus sp. cf. B. irradians

(Figures 16-17)

A single, nearly intact scutum from CASG locality 54135 is tentatively referred to *B. irradians.* It is thin, about as broad as high, and slightly concave externally between base and apex. The exterior bears closely spaced, semi-erect growth ridges that are finely crenate. The tergal margin is slightly reflexed and the basitergal angle is rounded. The articular ridge is convex, reflexed over the articular furrow, and protrudes beyond the tergal margin. The articular furrow is narrow, shallow, and short. The articular ridge is long, fully two-thirds the length of the tergal margin. A short, low, blunt adductor ridge is present along the margin of the large oval adductor muscle pit in the upper half of the scutum and is separated from the articular ridge. The depressor muscle pit is a large triangular area between the adductor muscle pit and the basitergal angle. This pit is not bordered by a ridge on its occludent side. The pit for the depressor muscles in the basioccludent angle is large, triangular, and deep.

This scutum bears some resemblance to those of *B. balanus* and *B. rostratus*, but differs from both in its greater breadth, thinness, its short, blunt adductor ridge that is well removed from the articular ridge, and in the greater size and depth of the depressor muscle pit that is not bordered by a ridge on its occludent side. This scutum differs from others found at CASG locality 54135 and identified as *Balanus* sp. aff. *B. nubilus* by its greater width, its convex rather than straight articular ridge that is much more reflexed and much longer, its shorter, blunter adductor ridge, and the lack of striations or ridges in the depressor muscle pit.

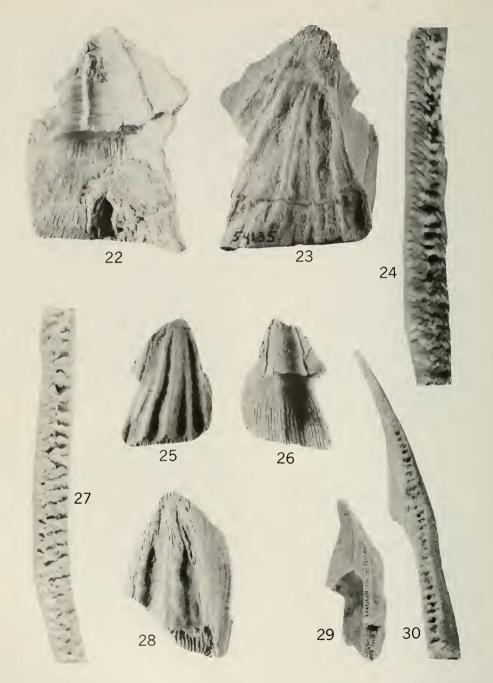
Balanus sp.

(Figures 31-33)

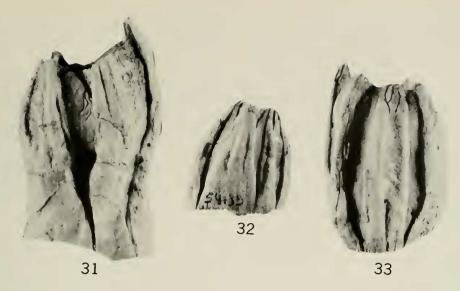
Several whole, high conic and cylindric shells cannot be identified beyond the generic level. Their orifices are toothed, the radii are moderately sunken with oblique summits, and the parietes are smooth to irregularly plicate, to inconspicuously ribbed. These shells may represent either *B*. sp. aff. *B. nubilus* or *Notomegabalanus*(?) *insperatus*, but their preservation is not conducive to the identification of specific characters.

Subfamily MEGABALANINAE Newman, 1980 Notomegabalanus(?) insperatus new species (Figures 22-30)

DIAGNOSIS.—Shell of six compartmental plates with broad, tubiferous radii; summits of radii oblique; septa of radial sutural edge bearing denticulae on lower sides only; exterior of parietes of larger compartmental plates with three to five prominent ribs, and ornamented by fine, closely spaced radial striae; parietal tubes numerous, rectangular, without transverse septa,



FIGURES 22-30. Notomegabalanus(?) insperatus new species. Figs. 22-24. Interior, exterior, and right radial sutural edge views of rostrum, holotype CASG 60914; greatest height of plate 36.4 mm. Figs. 25-26. Exterior and interior views of lateral plate, paratype CASG 60915; greatest height of plate 20.5 mm. Figs. 27-28. Radial sutural edge and exterior views of lateral plate, paratype CASG 60916; greatest height of plate 28.5 mm. Figs. 29-30. Side view and enlargement of radial sutural edge of lateral plate, paratype CASG 60917; greatest height of plate 18 mm.



FIGURES 31-33. Balanus sp., side views of three shells, hypotypes CASG 60911 through 60913, respectively; greatest height of shells: (Fig. 31) 42 mm, (Fig. 32) 20.5 mm, (Fig. 33) 29 mm.

but secondarily filled in upper half; basis unknown, but presumed calcareous; opercular plates unknown; distinguished from other species of *Notomegabalanus* Newman, 1980, and *Austromegabalanus* Newman, 1980, by the prominent external ribbing of the shell wall.

DESCRIPTION.—Reconstructed shell high conic with broad, tubiferous radii and moderately toothed orifice; summits of radii oblique; radial sutural edges septate, with septa bearing denticulae on lower sides only; alae moderately broad with oblique summits, confined to area of sheath; length of sheath less than one-half height of compartmental plates; lower margin of sheath free-standing, with shallow cavity between basal margin of sheath and interior of shell wall; exterior of parietes with from three to five prominent ribs on the larger compartmental plates, and ornamented by fine, closely spaced radial striae crossed by weak, widely spaced growth lines; interior of shell wall ribbed between base and sheath, internal ribs low, moderately developed, each corresponding to a parietal septum; parietal tubes numerous, without transverse septa, but secondarily filled in upper half; parietal septa thin, basally denticulate; outer lamina with one to four thin, half or quarter septa; basis unknown but presumed calcareous from basal denticulation of parietal septa; opercular plates unknown.

MATERIAL EXAMINED.—Twenty-four disarticulated compartmental plates and one possibly complete shell from CASG locality 54135.

TYPE MATERIAL.—Holotype, CASG no. 60914; paratypes, CASG nos. 60915 through 60918, and paratype lot CASG no. 60919 in the California Academy of Sciences paleontological type collection.

ETYMOLOGY.—The specific name is Latin for unhoped for or unexpected.

DISCUSSION.-Recently, Newman (1980) subdivided the genus Megabalanus Hoek, 1913, into three genera. Megabalanus s.s. includes most of the Megabalanus tintinnabulum (Linnaeus, 1758) complex together with related species of modern tropical and warm temperate seas. The two new genera, Austromegabalanus and Notomegabalanus, include fossil and extant species restricted to austral cool temperate and subpolar waters. The only obvious shell character separating Megabalanus s.s. from the two austral genera is that the septa of the radial sutural edge of Megabalanus are denticulate on both their lower and upper sides, whereas the septa of the austral genera are denticulate only on their lower sides. The two austral genera are separated on characters of their terga; that of Austromegabalanus has a beak and a closed spur furrow, whereas that of Notomegabalanus is not beaked and has an open spur furrow. There are features of the mouth parts as well that can be used to distinguish true Megabala*nus* from the austral genera, but when dealing with the generic assignment of fossil species, only shell and opercular plate characteristics are available.

The revision of *Megabalanus* proffered by Newman is sound, both from a systematic and biogeographic point of view. However, the Neogene fossil megabalanid record from California presents a problem. The species described here and "*Megabalanus*" wilsoni (Zullo, 1969a) from the Pliocene San Diego Formation have radial sutural dentitions characteristic of Newman's austral genera. Furthermore, the tergum of "*M.* wilsoni is typical of *Notomegabalanus*, although the spur furrow is closed in adult specimens, and its resemblance to that of *N. algicola* (Pilsbry, 1916) from South Africa was noted previously (Zullo 1969a).

The Notomegabalanus species closest geographically to the California coast is N. concinnus (Darwin, 1854) from the Peruvian province. This species was not included by Newman, but it has the sutural dentition, tergum, labrum, and protuberant lower margin of the first maxilla that characterize Notomegabalanus. Are these California Neogene species true Notomegabalanus derived from some austral, perhaps South American ancestor? Does the Austromegabalanus-Notomegabalanus complex represent an ancestral, previously worldwide stock from which tropical and warm temperate Megabalanus s.s. evolved? Or do the California species represent a separate group exhibiting convergence of characters with the austral genera? At present it is possible only to consider the California species on the basis of their morphologies and to assign them to Notomegabalanus on the characters delimiting that taxon. The association of N.(?) insperatus with a cool temperate fauna does, however, suggest affinities with the austral megabalanid genera.

Notomegabalanus(?) insperatus differs from all other megabalanid species in bearing distinct, prominent, external ribs. Megabalanus validus (Darwin, 1854) and M. zebra (Darwin, 1854) have ribbed shells, but their ribs are low, rounded, and usually confluent, rather than erect and separate. In addition, both of these species have the sutural dentition typical of Megabalanus s.s. This new species is questionably assigned to Notomegabalanus rather than to Austromegabalanus solely on the basis of the presence of another *Notomegabalanus*, *N. wilsoni*, in the California Neogene.

ACKNOWLEDGMENTS

We thank Peter Rodda, California Academy of Sciences, for information concerning the geologic setting and stratigraphy of the Wilson Ranch beds and for his review of the manuscript; and Barry Roth, California Academy of Sciences, for his assessment of the age and depositional environment of the Wilson Ranch molluscan fauna and for his review of the manuscript.

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